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**Landscape Ecology**

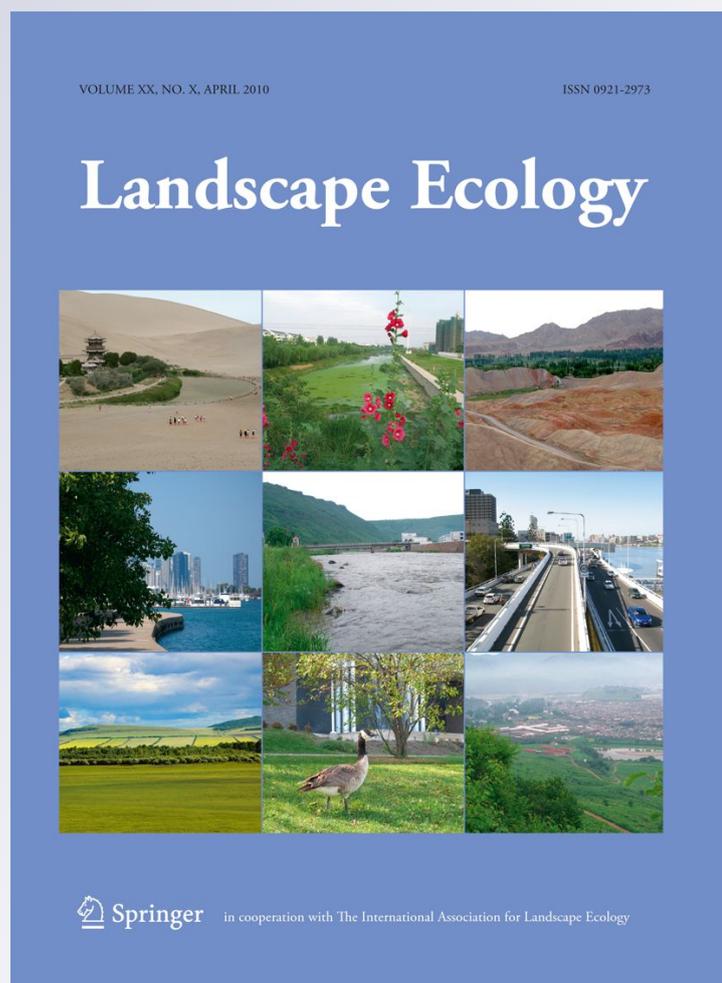
ISSN 0921-2973

Volume 27

Number 5

Landscape Ecol (2012) 27:633-640

DOI 10.1007/s10980-012-9727-2



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## Short perceptual range and yet successful invasion of a fragmented landscape: the case of the red-bellied tree squirrel (*Callosciurus erythraeus*) in Argentina

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Received: 23 May 2011 / Accepted: 13 February 2012 / Published online: 3 March 2012  
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**Abstract** Dispersal is a key element of the invasion process for introduced species, and is influenced by landscape connectivity. The red-bellied squirrel (*Callosciurus erythraeus*) was introduced to Argentina in 1970. Suitable forest habitat for this arboreal species is highly fragmented in a rural–urban matrix, but despite this, the squirrel population has spread. Squirrels disperse into new habitat patches using connective features such as forest corridors. They may also cross gaps but up to what extent is not known. Gap crossing success is influenced by perceptual range, which is the distance from which animals can perceive suitable habitat. Perceptual range has been previously estimated for vulnerable species, but not for introduced species. We used a model relating perceptual range to body mass to predict the perceptual range of the red-bellied tree squirrel in Argentina. We then tested our prediction of 202–221 m by releasing squirrels in an unfamiliar arable field at different distances (300, 200, 100 and 20 m) from woodland

habitat. We assumed that if woodland could be perceived, squirrels would orientate toward it. We estimated perceptual range to be between 20 and 100 m, considerably lower than predicted. Our results indicate that squirrels can potentially cross small habitat gaps, but dispersal over greater distances lacking connectivity is less likely. Incorporating this information when modelling the spread of exotic squirrels in the Pampas Region can yield more accurate prediction of the invasion process and guide management practices to minimise their expansion.

**Keywords** Dispersal · Invasive rodents · Landscape connectivity · Orientation · Translocation experiment

### Introduction

Within a heterogeneous landscape, the dispersal movements of individual animals between patches of suitable habitat are a major determinant of the persistence and distribution of populations (Hanski and Gilpin 1991; Leibold et al. 2004). The extent to which dispersal is assisted or impeded by landscape structure depends on the animal's behaviour and the scale at which it interacts with the landscape (Taylor et al. 1993; Wiens et al. 1993; Lima and Zollner 1996; Tischendorf and Fahrig 2000; Browne and Bowers 2004; Bélisle 2005). This scale is determined by perceptual range, defined as 'the distance from which

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a particular landscape element can be perceived as such (or detected) by a given animal' (Lima and Zollner 1996). Inherent in this definition is that the landscape element is important to the animal and the perceptual distance is habitat and species specific (Mech and Zollner 2002; Prevedello et al. 2011). Ability to perceive preferred habitat, and thus orientate toward it, is an important component of the navigation capacity of an organism (Nathan et al. 2008), allowing time spent in the hostile matrix to be reduced (Zollner and Lima 1997; Pe'er and Kramer-Schadt 2008; Prevedello et al. 2010).

Perceptual range has been estimated for vulnerable species to investigate how habitat fragmentation may limit dispersal and imperil population viability (e.g. Conradt et al. 2000; Zollner 2000; Schooley and Branch 2005; Flaherty et al. 2008; Forero-Medina and Vieira 2009; Prevedello et al. 2010). However, no studies have addressed perceptual range of introduced species, which may be a conservation concern from another perspective. Understanding dispersal ability of introduced species will help to explain and predict colonisation of new areas leading the invasion process (Neubert and Caswell 2000).

The red-bellied squirrel (*Callosciurus erythraeus*), a species native to South-east Asia, has been introduced to Argentina, Belgium, France, the Netherlands, and Japan (Jouanin 1986; Setoguchi 1990; Aprile and Chicco 1999; Dijkstra et al. 2009; Stuyck 2009). Evidence suggests that this species negatively affects native birds and squirrels and also causes economic damage through bark-stripping and consuming fruit in plantations, and gnawing property such as electric cables and sprinkler systems (Azuma 1998; Pereira et al. 2003; Miyamoto et al. 2004; Guichón et al. 2005; Dijkstra et al. 2009; Stuyck 2009; Benitez et al. 2010). Despite this, pet shop trade and intentional releases of this charismatic sciurid repeatedly create new foci of invasion (Guichón et al. 2005), facilitated by its ability to establish new populations from just 2–5 individuals (Bertolino 2009).

Red-bellied squirrels are highly arboreal, showing strong aversion to the ground (Chou et al. 1985). In the Pampas Region of Argentina, the native vegetation is grassland, but this has been heavily modified by agriculture and urbanisation (Bárbaro 1994). No native squirrels are present and the red-bellied squirrels inhabit a sparse mosaic of introduced arboreal vegetation composed of woodlands planted for timber,

fruit production or ornamental purposes in rural and urban areas (Guichón and Doncaster 2008). Despite high fragmentation of suitable habitat, squirrels have invaded over 1,300 km<sup>2</sup> since their introduction in the 1970s (Benitez et al. 2010). Aside from occasional human-mediated dispersal, red-bellied squirrels can invade new woodland patches either by dispersing through the use of connective features such as trees planted along fences, roads and railways (forested corridors) or, by crossing open areas. Use of connective features has been observed, but it is not known what distances squirrels may cross in open areas, where predation risk from raptors and domestic dogs is high (ML Guichón pers. obs.). Determining the perceptual range of this species when moving through open landscapes would provide vital information for predicting more accurately the local-scale patterns of population spread and setting management strategies accordingly.

Perceptual range has been investigated in other sciurid species, which like the red-bellied tree squirrel rely mainly on visual cues to discern habitat (Thorington and Ferrell 2006). Zollner (2000) used a method of release within unfamiliar open habitat at different distances from woodland to measure perceptual range for three species. Estimates were observed to scale with average species body mass, allowing perceptual range to be predicted for a given species (Mech and Zollner 2002). We used this model to predict perceptual range for red-bellied squirrels in Argentina, and empirically tested the prediction using an experimental approach similar to that of Zollner (2000).

## Methods

### Predicting perceptual range and selecting release distances

Mech and Zollner's (2002) model to predict perceptual range for mammals from their body mass incorporates two equations. Equation 1 calculates the slope of the species regression (S) from the average mass (M) of the species.

$$S = 0.53839 - 0.00052M \quad (1)$$

Equation 2 uses S to predict the perceptual distance (D) from a given habitat horizon height (H). The

critical angular divergence (ADcrit) is a range from 63° to 69° within which the average angular divergence of a species' movement path in relation to the nearest forest edge (defined as zero) was found to become non-significant.

$$D = (\text{ADcrit} \div S) (H \div 15.5) \quad (2)$$

The average weight of red-bellied squirrels captured in our study was 250 g  $\pm$  28 (SD) (average weight recorded for the population in Argentina is 260 g  $\pm$  37, Cassini and Guichón 2009). The height of the woodland patch was approximately 20 m yielding a predicted perceptual range of 199–218 m for the squirrels we released (192–210 and 206–226 m accounting for  $\pm$ SD of body weight). The underlying assumption of this experimental procedure is that animals released into an inhospitable environment will orientate and move toward preferred habitat if they are able to perceive it. We released squirrels at distances of 100, 200 and 300 m and expected that they would be unlikely to perceive and orientate toward the woodland patch at 300 m, may do it at 200 m and would orientate toward woodland at 100 m. A further release distance of 20 m was used to test the validity of the method.

### Estimating perceptual range

#### Study area

The study area was located in North-eastern Buenos Aires province, Argentina, close to Luján city (34°36'S, 59°11'W), where the main population of red-bellied squirrels has established since their introduction (Aprile and Chicco 1999) (Fig. 1). The release experiment took place between June and November 2007 in a flat agricultural field of approximately 250 ha that contained four small patches of woodland (Fig. 1c). We selected the most isolated patch (>800 m from other trees), which was 0.7 ha mainly composed of *Eucalyptus* sp. and *Gleditsia triacanthos*. The field had been used to grow soy but the experiment took place after harvest when bare soil, dry matter and short (<15 cm) herbaceous vegetation resulted in a homogenous terrain. Squirrels already populated woodland surrounding the field therefore this study did not assist the spread of this species into new areas.

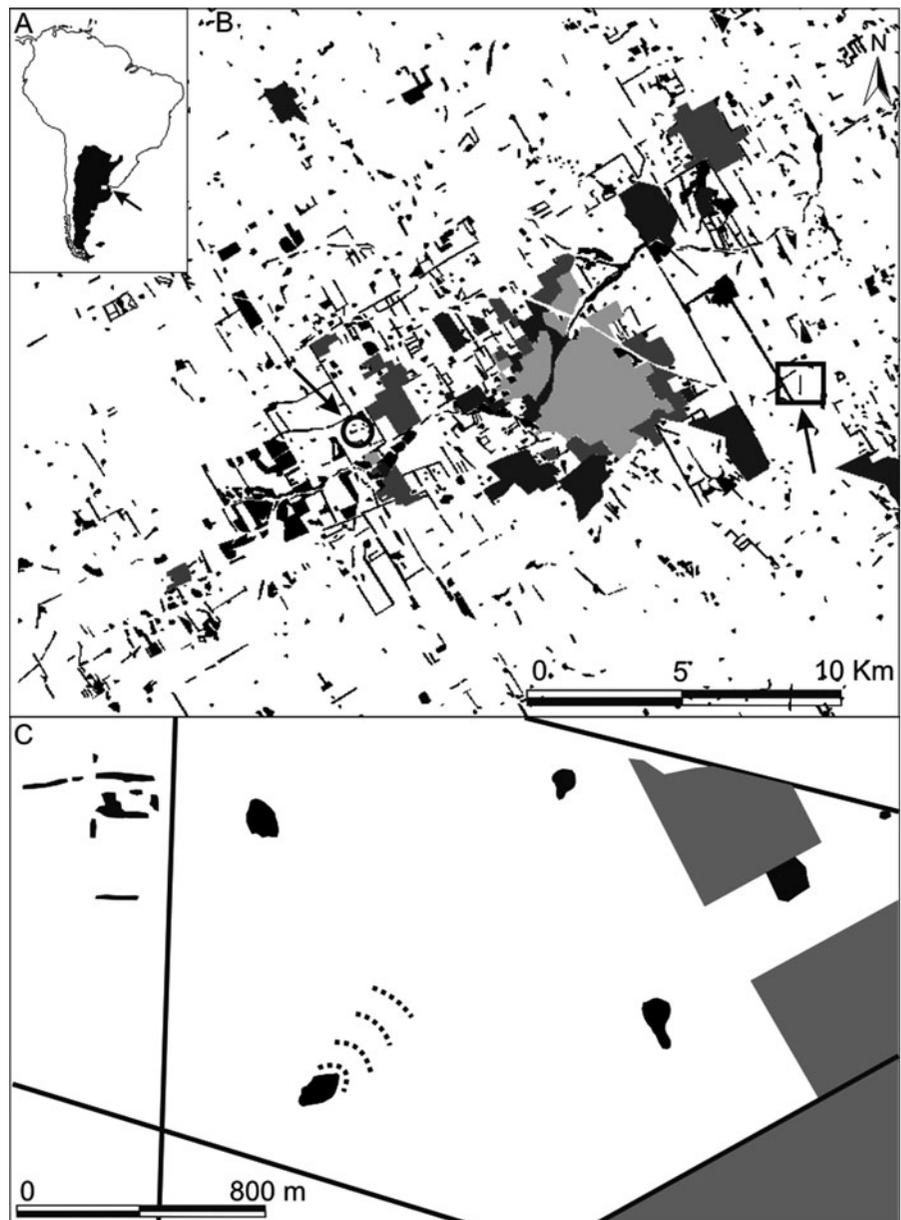
### Experimental procedure

We captured red-bellied squirrels in residential areas >2 km from the release site, which we assumed to be unfamiliar to these animals given the relatively small home ranges of this species (0.28–2.2 ha, Tamura et al. 1989). We set baited cage traps (30  $\times$  13  $\times$  13 cm) on tree branches each morning and released squirrels on the day of capture. We transported them to the release site within their trap, which was covered with a dark cloth to minimise stress and to prevent viewing of the surroundings. One or two releases occurred per day and each squirrel was randomly allocated to a different release point spaced 15 m apart at one of the four release distances. Releases from different points were carried out to reduce chances of squirrels following trails left by previously released animals and we observed no evidence of movement being influenced in this way. Release points were >500 m from other woodland (Fig. 1c), a distance of more than double the predicted perceptual range, so we assumed squirrels would not perceive these patches.

We sexed and weighed squirrels, and marked them with a fur clip whilst they were restrained using a funnel-shaped cloth handling device. We painted the underside and tail of each animal with non-toxic fluorescent orange powder (Capricorn Ltd; Lemen and Freeman 1985). Squirrels were then placed inside a circular wire cage (26  $\times$  13 cm) covered with a dark cloth. The circular design of the cage, which had a hole on the underside closed with a sliding trap door, gave the animals a 360° view of their surroundings before and during exiting. We secured the wire cage to the top of a 1.5 m ladder to simulate an elevated position as expected for this arboreal species. If squirrels made movement decisions prior to climbing down to the ground, the slight elevation could increase their perceptual range beyond that predicted by the model. The effect of elevation on perceptual range has not been explored in other studies.

Squirrels were released by pulling away the cloth and sliding trap door using a long piece of string from a hide situated within the woodland, approximately 20 m from the edge. From this hide we observed the behaviour of the animals using a telescope (60 $\times$ ) and recorded the time taken to leave the release point. Observations of squirrels moving toward woodland, apparently oblivious of or undeterred by the hide, supported the assumption that it had little or no effect

**Fig. 1** **a** Location of the study site in Argentina. **b** Map showing suitable habitat for squirrels (woodland habitat in *black* and residential, suburban and urban habitats in shades of *grey* of decreasing intensity) and the matrix of unsuitable habitat (unforested areas in *white*) (re-drawn from Guichón and Doncaster 2008). The original release point of the squirrels in 1970 is indicated with a *circle*, and the area of the release experiment with a *square*. Squirrels have colonized the entire area depicted. **c** Area of the release experiment showing forested patches and roads in *black*, residential areas in *grey*, and approximate location of release points of squirrels at 20, 100, 200 and 300 m (*dotted lines*) from the focal forested patch. (Color figure online)



on their behaviour. After dark, we followed fluorescent UV powder trails left by the squirrels using a UV light. Trails were recorded using a GPS (Etrex Legend Garmin Ltd) marking tracks and waypoints (accuracy 3–5 m), until they became too faint to detect or until the woodland was reached.

#### Data analysis

We measured the perceptual ability of squirrels by determining whether they were orientated toward the

woodland after moving a prescribed distance, which was long enough to allow for a period of orientation (Zollner and Lima 1997; Zollner 2000), but shorter than the distance to the woodland to avoid possible random wandering (Goodwin et al. 1999). We assumed that the period of orientation would be minimal in our study because the circular cage allowed unbiased orientation decisions. Therefore, for all releases we measured angles of orientation, relative to  $0^\circ$  as the vector of shortest distance to the woodland, at the 8 m point of the trail (“short trails”) using GPS

Trackmaker software. To test that squirrels did not become more orientated toward woodland as they moved, we also measured orientation at a point farther along the trail (“long trails”) for releases at 100, 200 and 300 m. Whenever possible we used the 40 m point for long trails. We excluded from this analysis a short, 8 m trail and used the maximum distance recorded (13–30 m) for four other trails.

We analysed whether squirrel movements were orientated toward woodland using V-test circular statistics, which are suitable for small sample sizes (Batschelet 1981). Rayleigh tests were also used to detect any significant orientation in directions other than the woodland (Fisher 1993). The possibility of sex-related differences in orientation was examined using Mardia–Watson–Wheeler pair-wise tests (Batschelet 1981). We analysed whether the time taken to leave the release cage was dependent on release distance using a simple linear regression following a logarithmic transformation  $[\log(y + 1)]$  of the response variable.

**Results**

In total, 37 red-bellied squirrels were released, 8 at 300 m (4 females, 4 males), 9 at 200 m (3 females, 6 males), 9 at 100 m (3 females, 6 males) and 11 at 20 m (3 females, 8 males) from the woodland. Average weight of the squirrels was similar between males (248 g ± 32 (SD)) and females (255 g ± 21 (SD)). No difference was found between the angles of orientation of male and female squirrels either for short trails (Mardia–Watson–Wheeler;  $W = 0.643$ ,  $p = 0.725$ ) or for long trails (Mardia–Watson–

Wheeler;  $W = 1.001$ ,  $p = 0.606$ ) so we pooled data for further analysis.

Analysis of short trails revealed that squirrels were not significantly orientated toward the woodland at 300, 200 or 100 m (Table 1; Fig. 2). Orientation toward woodland was significant only for squirrels released at 20 m. Squirrels were not orientated toward woodland when analysing long trails for the three farther release distances (Table 1). Therefore no preferred movement direction was observed for squirrels released at 200 m, which was close to their predicted perceptual range, or even at 100 m. Squirrel movement did not show significant orientation in any direction regardless of woodland position at the three larger release distances (Table 1).

Time taken for squirrels to leave the release cage ranged from 0 to 114 min. Squirrels left the release cage more readily at larger than shorter distances from the woodland (slope =  $-0.0018 \pm 0.002$ ,  $F = 5.260$ ,  $df = 35$ ,  $p = 0.028$ ,  $R^2 = 0.13$ ), though high variability was observed at each release distance (mean ± SD at 20 m:  $33.18 \pm 25.58$  min; 100 m:  $32.44 \pm 38.71$  min; 200 m:  $14.33 \pm 20.62$  min; 300 m:  $12.88 \pm 10.48$  min). The squirrels that we observed reaching the woodland, including 1–2 individuals released at each 100, 200 and 300 m, covered the distance in <5 min.

**Discussion**

We experimentally contrasted the field measured perceptual range of red-bellied squirrels with that predicted from the Mech and Zollner (2002) model and to our knowledge this is the first study dealing with

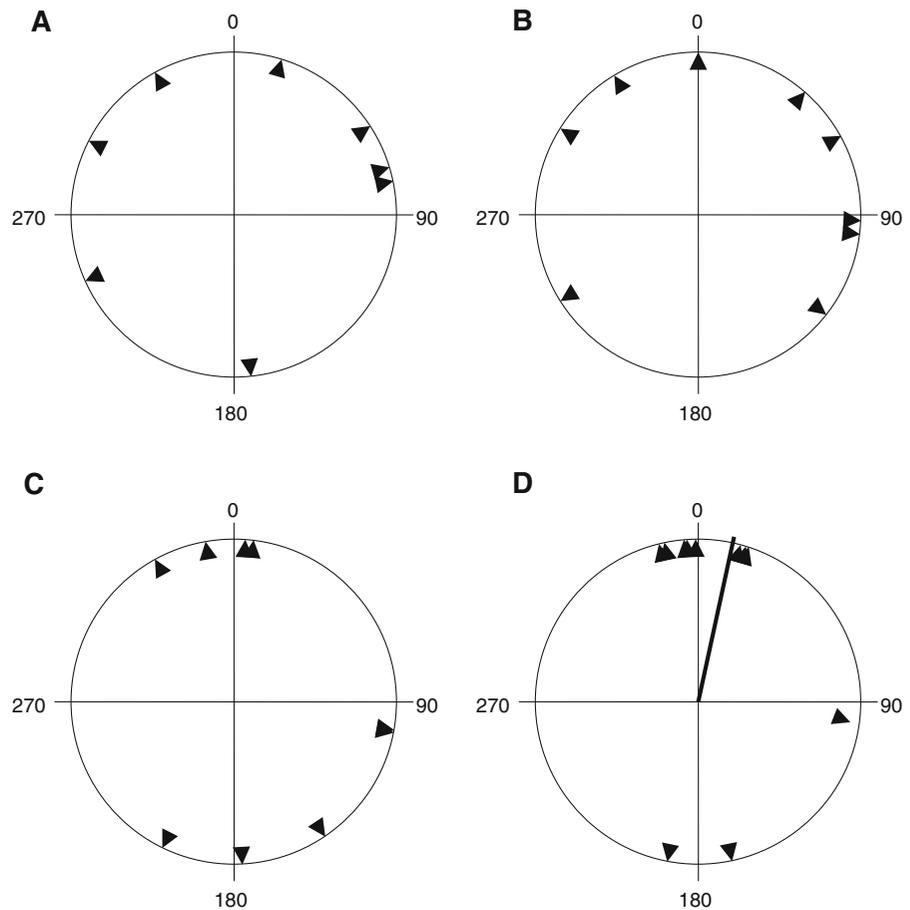
**Table 1** Mean angular divergence (°) and 95% confidence intervals of the movement paths of red-bellied squirrels after short (8 m) and long (40 m) trails and the results of V-tests

Release distance (m)	Angular divergence		Orientation toward woodland				Orientation in any direction			
	Short	Long	Short		Long		Short		Long	
	Mean	Mean	<i>u</i>	<i>p</i>	<i>u</i>	<i>p</i>	<i>Z</i>	<i>p</i>	<i>Z</i>	<i>p</i>
300	75.6 ± 41.5	77.8 ± 44.0	0.964	0.172	0.917	0.184	0.562	0.585	0.496	0.624
200	70.0 ± 33.0	65.1 ± 43.9	1.096	0.140	1.329	0.094	1.090	0.346	0.936	0.404
100	81.6 ± 54.3	78.7 ± 50.4	0.358	0.363	0.565	0.290	0.375	0.699	0.427	0.665
20	50.5 ± 47.6		2.344	0.009						

used to determine whether squirrels were orientated toward woodland and Rayleigh tests used to determine orientation in any direction

Squirrels were released within an arable field at different distances from the woodland

**Fig. 2** Angles of orientation of red-bellied squirrels from their point of release (centre of the *circle*) at **a** 300 m, **b** 200 m, **c** 100 m and **d** 20 m from a woodland patch, to their location after short trails (8 m of movement). Each *triangle* represents the location of an individual squirrel. Angles are calculated in relation to a vector of 0° to the woodland patch. Significant orientation is represented by the *solid vector*



the orientation of an invasive species. Squirrels did not orientate toward woodland at the predicted perceptual distance close to 200 m, nor even at 100 m, and they preferentially moved toward the woodland only when released at 20 m, though they showed no greater motivation to leave the release cage based on time. Therefore, perceptual range of this species would be within 20–100 m. Estimated perceptual range was low compared to predicted despite releasing squirrels from an elevated cage, which could potentially have improved perceptual distance. Further work is required to determine how elevation influences perceptual abilities of tree squirrels. Our results are consistent with Forero-Medina and Vieira (2009) and Flaherty et al. (2008), who also observed a shorter perceptual distance than predicted based on Mech and Zollner's (2002) equation (Table 2).

Mech and Zollner (2002) acknowledge that their equation is a starting point for predicting perceptual range, which may also be influenced by other intrinsic

characteristics of the species and extrinsic factors such as wind direction and speed, and matrix vegetation (Schooley and Branch 2005; Flaherty et al. 2008; Forero-Medina and Vieira 2009; Prevedello et al. 2010). Though we did not test the influence of wind on movement decisions, we do not consider that this played a significant role as sciurids are thought to use visual cues to discern habitat (Thorington and Ferrell 2006). Our results indicate that no landscape element other than the woodland influenced our results, as no alternative preferred orientation was observed. It is also unlikely that matrix structure reduced perceptual range (Flaherty et al. 2008; Prevedello et al. 2011) because we released squirrels within a highly homogeneous field with very short vegetation. The longer time taken to leave the cage at shorter distances could be related to navigation processes (Nathan et al. 2008) when woodland habitat is perceived.

Short perceptual range indicates that red-bellied squirrels are unlikely to successfully disperse >100 m

**Table 2** Summary of predicted and estimated perceptual range

Species	Average body weight (g)	Height of habitat used	Predicted perceptual range (m)	Estimated perceptual range (m)	Reference
Fox squirrel ( <i>Sciurus niger</i> )	787	15.5	472–517	400–500	Zollner (2000) and Mech and Zollner (2002)
Gray squirrel ( <i>Sciurus carolinensis</i> )	510	15.5	223–244	300–400	Zollner (2000) and Mech and Zollner (2002)
Eastern chipmunk ( <i>Tamias striatus</i> )	109	15.5	127–138	120–180	Zollner (2000) and Mech and Zollner (2002)
White-footed mouse ( <i>Peromyscus leucopus</i> )	21	15.5	116–127	90–120	Zollner and Lima (1999) and Mech and Zollner (2002)
Grey four-eyed opossum ( <i>Philander frenatus</i> )	395	31	378–414	100–200	Forero-Medina and Vieira (2009)
Woolly mouse opossum ( <i>Micoureus paraguayanus</i> )	114	31	262–287	100–200	Forero-Medina and Vieira (2009)
Northern flying squirrel ( <i>Glaucomys sabrinus</i> )	130	37.7	325.5–356.5	100–150	Clearcuts, Flaherty et al. (2008)
		18.5	159.7–174.9	25–50	Second-growth stands, Flaherty et al. (2008)
Red-bellied squirrel ( <i>C. erythraeus</i> )	260	20	202–221	20–100	This study

Predictions are based on Mech and Zollner's (2002) equation and the first four species were used to develop the equation. Estimations were made by releasing animals into inhospitable habitat at different distances from preferred habitat patches and analysing movement trajectories

across unforested areas within the Pampas. The successful invasion of fragmented woodland habitat by squirrels must therefore be explained by short-distance dispersal across open areas of <100 m, or via connective features such as forested corridors. Future research to better understand what features increase the functional connectivity of the landscape for this species will help explain colonisation patterns. For example, if squirrels avoid the ground, but readily move relatively long distances along fences and overhead cables they may disperse into habitat patches that appear otherwise isolated in Fig. 1.

Continued spread of red-bellied squirrels could lead to colonisation of forests of high biodiversity, threatening native birds and squirrels. In these circumstances, reducing connectivity could be considered as a tool to limit spread, though any negative effects on native species must be explored. Our results suggest that long-distance dispersal of red-bellied squirrels into isolated forested areas is unlikely except where it is mediated by humans. Deliberate transport and release of these charismatic animals is a serious concern that is being addressed by on-going education of local communities about the negative effects of introduced species. All these elements should be

considered in future predictions of invasion dynamics and design of control actions.

**Acknowledgments** We thank Dr Fernando Milesi for his valuable input and help with trapping squirrels, Cecilia Gozzi, Lucas Miranda and Laura Messetta for assistance with field trials, the Luján residents who allowed us to trap squirrels on their property, and two anonymous reviewers for their constructive criticism on the manuscript. We also thank The Natural Environment Resources Council (LJB), CONICET (VVB and MLG) and the Universidad de Luján for funding, and Capricorn Ltd. for supplying free fluorescent powder samples vital for tracking squirrel movement.

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